

REVISION OF THE FAMILY LINEOLARIIDAE ALLMAN, 1864 (HYDROZOA: HYDROIDA)

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The family Lineolariidae Allman, 1864 is redefined and the known species are redescribed. The genus *Lineolaria* Hincks, 1861 is endemic to south-eastern Australia, and the new genus *Nicoliana* is proposed for *Lineolaria gravierae* Millard, 1975 from southern Africa. *Lineolaria parasitica* Antsulevich, 1987 and *Agglutinaria operculata* Antsulevich, 1987 from the Sea of Okhotsk are excluded from the family. *Lineolaria spinulosa* Hincks, 1861 and *Nicoliana gravierae* are both obligate epiphytes of scagrasses, and *Lineolaria flexuosa* Bale, 1884 occurs only on algae. Evolutionary implications and the distribution of the family are discussed.

THE FAMILY Lineolariidae presently comprises six species in two genera: *Lineolaria spinulosa* Hincks, 1861 (type species), *L. flexuosa* Bale, 1884, *L. inarmata* Blackburn, 1938, *L. gravierae* Millard, 1975, *L. parasitica* Antsulevich, 1987 and *Agglutinaria operculata* Antsulevich, 1987. *L. spinulosa*, *L. flexuosa* and *L. inarmata* are known from south-eastern Australia (Hincks 1861, Bale 1884, Bartlett 1907, Blackburn 1938, Watson 1973), and *L. flexuosa* has been reported also from New Zealand (Trebilcock 1928, Ralph 1958). *L. gravierae* is known from Madagascar and Mozambique (Gravier 1970, Millard 1975), and *L. parasitica* and *A. operculata* from the Sea of Okhotsk (Antsulevich, 1987).

Hincks (1861) (and later Stechow 1923) assigned *Lineolaria* to the Sertulariidae, but Allman (1864) introduced the family Lineolariidae to accommodate the genus and this classification was followed by Ralph (1958), Watson (1973) and Antsulevich (1987). Although Millard (1975: 133) and Bouillon (1985: 130) referred *Lineolaria* to the Campanulinidae, their definitions of the genus included a hydrothecal operculum "present or absent, when present membranous . . .", thus implying the possibility of a simple opercular flap, a structure inconsistent with the segmented operculum diagnostic of the Campanulinidae. In his original description of *Lineolaria*, Hincks (1861) made no mention of a hydrothecal operculum. I have examined Hincks's type material of *L. spinulosa* in the collection of the Natural History Museum, London (BMNH 1899.5.1.219) and, although no operculae are visible, their absence is readily explained by loss through drying. Young hydrothecae of fresh material that I have collected from lower

Port Phillip Bay all possessed an elliptical bilobed margin closed by a delicate membranous flap that is torn aside upon emergence of the young hydranth.

Antsulevich's (1987) diagnosis of the Lineolariidae includes a rudimentary hydrothecal peduncle to accommodate *L. parasitica* and *A. operculata* in the family. However, if Hincks's original concept of a sessile hydrotheca is to be maintained, these two species must be excluded. The inoperculate *L. parasitica* appears to have closer affinities with the Lafoeidae than with the Lineolariidae, while *A. operculata* with its conical operculum may be more closely related to *Cuspidella*, *Egmondella* or *Lafoeina*. Neither species, however, can be referred with confidence to any known genus until the reproductive structures are found.

A redefinition of the scope of the families Lineolariidae and Campanulinidae thus becomes necessary. If *Lineolaria* as understood by Millard (1975) and Bouillon (1985) is to remain in the Campanulinidae, then the Lineolariidae and Campanulinidae must be regarded as synonymous, with the name Lineolariidae taking precedence (Calder 1991). However, if the Lineolariidae is redefined to accommodate the operculum, the family may then be retained as distinct from the Campanulinidae. Since *Lineolaria* possesses a simple operculum in the type species, the new genus *Nicoliana* is introduced here to accommodate the southern African species with a segmented operculum.

Family LINEOLARIIDAE Allman, 1864, amended

Diagnosis. Small thecate hydroids with stolonial colonies growing on an underlying sheet of per-

isarc. Hydrotheca sessile, deep, tubular to saccate, with an upturned, untoothed or lobate margin; operculum a simple flap or conical, of converging segments demarcated from the margin. Hydranth slender and extensile, with a ring of filiform tentacles. Nematophores present or absent. Gonotheca sessile, gonophore a fixed sporosac.

Lineolaria Hincks, 1861, amended

Type species. Lineolaria spinulosa Hincks, 1861.

Diagnosis. Colonies stolonial, hydrotheca sessile, deep, cylindrical to saccate, margin upturned, elliptical to circular with two opposite lobes and an operculum of a simple flap. Nematophores absent. Gonotheca sessile, gonophore a fixed sporosac.

Lineolaria from Australia and New Zealand. The type material of *L. spinulosa* is epiphytic on dried leaves of the seagrass *Cymodocea antarctica* (= *Amphibolis antarctica* (Labill.) Sonder et Aschers) and is labelled "Geelong, Australia". It is from a "parcel of sea-weed . . . from the neighbourhood of Melbourne and Geelong" (Hincks 1861). The type locality given is probably incorrect since the nearest occurrence of *A. antarctica* to Melbourne and Geelong is in lower Port Phillip Bay and Bass Strait. The species has been recorded from the same substrate at other localities by Bale (1884), Bartlett (1907), Blackburn (1938) and Watson (1973 and present study). It is the most abundant hydroid epiphyte of *A. antarctica* (Watson in press) and is an equally common epiphyte of *Posidonia australis* (Hooker) and *P. sinuosa* Kuo & Cambridge in south-eastern Australia (J.E.W. unpubl.). Despite extensive searching I have not found the species on other substrates nor on the same species of seagrasses in south-western Australia.

Lineolaria flexuosa is a south-eastern Australian algal epiphyte, found in this study to be chiefly associated with the common brown alga *Sargassum* spp. and the red alga *Rhodymenia*. *L. flexuosa* has been recorded in Australia from the environs of Port Phillip Bay (Bale 1884, Bartlett 1907) and from the Sir Joseph Banks Islands in Spencer Gulf (Blackburn 1938). The only previous record of substrate is of a specimen "on alga" from Williamstown, Victoria (Bale 1884). Material on algae from West Island, South Australia, identified as *L. spinulosa* by Shepherd & Watson (1970), is also probably *L. flexuosa*. Despite the paucity of records I have

found *L. flexuosa* to be a moderately common algal epiphyte; it is not, however, as abundant as *L. spinulosa*.

Trebilcock (1928) recorded *L. flexuosa* from Stewart Island in southern New Zealand without describing the specimen or commenting upon its habitat. Despite careful search of the Trebilcock collection and other material in the Museum of Victoria, I have found no specimen corresponding to Trebilcock's data. Ralph (1958) also recorded *L. flexuosa* from Cape Maria Van Diemen, New Zealand, growing on the stem of *Synthecium*. Because the specimen was sterile she described and figured a gonotheca from a microslide preparation of *L. flexuosa* from the Sir Joseph Banks Islands, Australia, prepared by M. Blackburn and now in the collection of the Museum of Victoria. I have examined two microslides of the Cape Maria Van Diemen specimen (loaned by Dr P. M. Ralph) and found that the hydrothecae, all of which are partially free of the substrate, have an entire, more or less circular margin, not the distinctively lobed, usually elliptical margin typical of *Lineolaria*. None of the specimens shows any evidence of there having been an operculum. Since partially adnate, cylindrical hydrothecae with circular margins and without operculae are typical of *Filellum*, I believe that Ralph's specimens should be referred to that genus. This view is supported by the epizoid habit of the specimen on *Synthecium*, a favoured substrate of *Filellum* in southern Australian waters (J.E.W., unpubl.). This is in contrast with the epiphytic habit of the *Lineolariidae*.

Lineolaria inarmata has been recorded only once, from seagrasses at the type locality at the Sir Joseph Banks Islands in southern Spencer Gulf, South Australia. I have examined the holotype (NMV F57878) and paratype (NMV F57879) microslides (Canada balsam mounted) in the collection of the Museum of Victoria and found the specimen to be closely similar to *L. spinulosa*. Blackburn (1938) distinguished between the two species chiefly on the absence of the basal hydrothecal spine in *L. inarmata* and the poorly developed marginal lobes of the hydrotheca. Detailed examination revealed that both the basal spines and the marginal lobes were in fact present but had been crushed in mounting. Blackburn further distinguished *L. inarmata* from *L. spinulosa* on ecological grounds, stating that *L. spinulosa* occurred only on *Cymodocea* (= *Amphibolis*), whereas *L. inarmata* was found only on *Posidonia*. This differentiation is no longer valid as *L. spinulosa* is now

found to be an equally common epiphyte of *Posidonia* in the Great Australian Bight (Watson 1973) and many other southern Australian localities (J.E.W. unpubl.). Thus *L. inarmata* is here considered a synonym of *L. spinulosa*.

The redescrptions of *L. spinulosa* and *L. flexuosa* given below are from fresh and preserved material and microslides. Measurements of both species are given in Table 1. Material used in this study has been deposited in the Museum of Victoria (registration numbers prefixed NMV).

Lineolaria spinulosa Hincks, 1861

Fig. 1A,B

Lineolaria spinulosa Hincks 1861: 280, pl. 8.—Allman 1864: 36.—Bale 1882: 8.—Bale 1884: 61, pl. 1, figs 10, 11, pl. 19, fig. 38.—Lendenfeld 1885a: 405.—Lendenfeld 1885b: 622.—Lendenfeld 1887: 18.—Bartlett 1907: 41.—Watson 1973: 165.

Lineolaria inarmata Blackburn 1938: 321, figs 4–8.

Material and records. NMV F51784, Queenscliff, Victoria, on *Amphibolis antarctica*, 3 m, J. E. Watson, 4 Jan. 1987, preserved material. NMV F51785, Gulf St Vincent, South Australia, on *Posidonia*, 16 m, S. A. Shepherd, 10 Nov. 1968, microslide.

Description. Hydorhiza broad and flat, reticulated; strongly adherent to the substrate. Hydrothecae borne directly on the hydorhiza, usually alternate, normal to the stolon and about 0.5–1 mm apart. Hydrotheca rectangular, perisarc with minute transverse striations, strongly adnate to the substrate for most of length then bending sharply upwards and becoming free in the distal fifth, slightly inflated proximally, narrowing slightly behind margin. Margin oval

with two small lateral lobes, immature hydrotheca closed by a delicate membranous flap. Base of the hydrotheca with a strong, erect chitinous spine at junction with hydorhiza, a small crease in the stolon opposite the spine.

Hydranth with about 16 tentacles, capable of withdrawing deeply into the hydrotheca.

Colonies dioecious, gonothecae large, abundant, usually nestled beside the hydrothecae between stolon reticulations, male and female similar in shape and size, flattened, irregularly ovate, adnate to the substrate by a peripheral flange about 0.1 mm wide. Aperture distal, circular or sub-circular, facing upwards with a thickened rim and closed by a membranous operculum. Surface of gonotheca with 16–30 small chitinous spines in three or four vaguely defined longitudinal rows, a mass of tissue surrounding the base of each spine. Gonophore irregularly ovate, the female comprising up to 15 ova arranged in two rows.

Colour. Trophosome transparent and colourless, so that the colony is almost invisible on the substrate. Gonophores cream-coloured.

Remarks. *L. spinulosa* is a minute hydroid, the colonies scarcely exceeding a height of 0.5 mm above the substrate. Contact with the substrate is by means of a very delicate, strongly adherent film of perisarc that underlies the entire colony. The thorn-like spines at the base of the hydrothecae are the same as those on the gonotheca. These robust, hollow chitinous structures are closed at the tip; unlike the tubular nematophores of *Nicoliana gravierae*, they do not con-

	<i>L. spinulosa</i>		<i>L. flexuosa</i>	
	Range	Mean	Range	Mean
Hydorhiza:				
maximum width excluding flange		0.17		0.08
Hydrotheca:				
length adnate	0.27–0.35	0.30	0.23–0.28	0.25
length free	0.06–0.09	0.08	0.04–0.08	0.06
maximum width	0.13–0.18	0.16	0.09–0.13	0.11
width at aperture	0.13–0.17	0.15	0.08–0.11	0.09
Gonotheca:				
length including flange	1.25–1.50	1.40	0.88–1.00	0.94
width including flange	0.63–0.75	0.68	0.55–0.75	0.65
diameter of aperture	0.14–0.18	0.16	0.15–0.20	0.18
maximum length of spine		0.08		0.08
width of spine at base		0.04		0.05

Table 1. Comparative measurements (mm) of *Lineolaria spinulosa* and *Lineolaria flexuosa* (n = 10, both species).

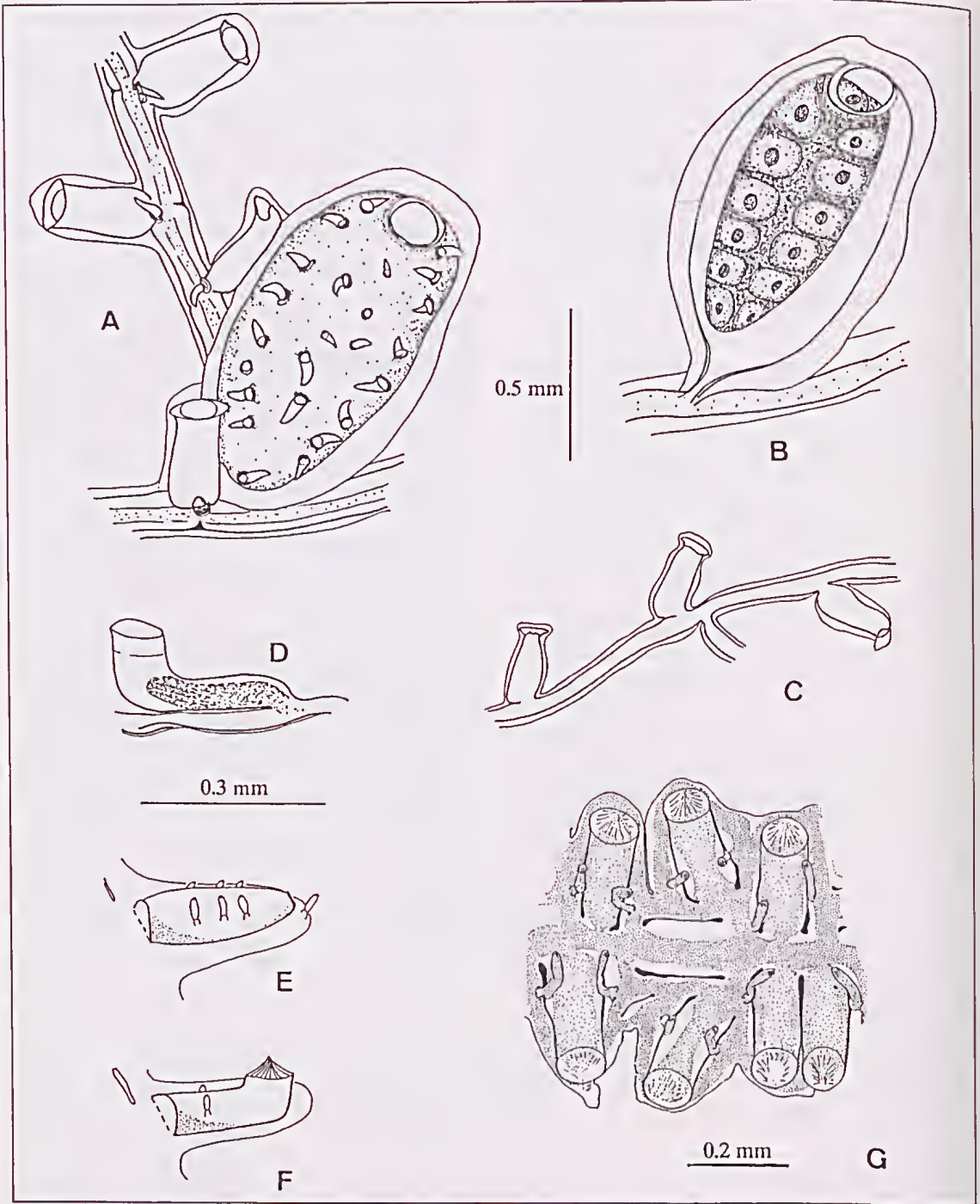


Fig. 1. A, B, *Lineolaria spinulosa*, colony from *Amphibolis antarctica*, Queenscliff, Victoria. A, part of colony with empty gonotheca. B, female gonophore inside gonotheca (gonothecal spines not shown). C, D, *Lineolaria flexuosa*, colony from *Sargassum*, Western Port, Victoria. C, part of sterile colony. D, hydrotheca without marginal lobes, resembling *Filellum*. E–G, *Nicoliana gravierae*. E, lateral view of gonotheca. F, lateral view of hydrotheca. E and F after Millard 1975. G, colony, after Gravier 1970 (scale not given).

tain nematocysts. It is possible that they were once also nematophores but with evolutionary loss of nematocysts have degenerated into spines. These may now serve as structures for passive defence of the colony.

L. spinulosa is an extremely fecund species, the colonies becoming fertile soon after earliest stolonisation. The marked irregularities seen in the walls of the gonothecae usually result from obstructions to free growth among the hydrorhizal reticulations.

Lineolaria flexuosa Bale, 1884

Fig. 1C, D

Lineolaria flexuosa Bale 1884: 62, pl. 1, figs 7-9.—Bale 1887: 19.—Lendenfeld 1885a: 405.—Lendenfeld 1885b: 622.—Lendenfeld 1887: 18.—Hartlaub 1905: 617.—Bartlett 1907: 41.—Trebilcock 1928: 8.—Blackburn 1938: 321.—Blackburn 1942: 111.—Smith & Watson 1969: 109.
non *Lineolaria flexuosa*.—Ralph 1958: 325, fig. 8a-h.—Shepherd & Watson 1970: 140.

Material and records. NMV F51786, Popes Eye Reef, Port Phillip Bay, Victoria, on *Zonaria*, 7 m, J. E. Watson, 31 May 1976, microslide. NMV F51787, Eagle Rock, Western Port, Victoria, on *Sargassum*, 3 m, J. E. Watson, 11 Nov. 1968, microslide. NMV F51788, Crawfish Rock, Western Port, Victoria, on *Rhodymenia*, 8 m, J. E. Watson, 26 Apr. 1969, microslide.

Description. Hydrorhiza flattened, adherent to substrate, with a small peripheral flange. Hydrothecae usually alternate and set at an acute angle to the stolon or parallel with it, connected to the stolon canal through a wide orifice. Hydrotheca rectangular to saccate, widest about the middle, adnate to substrate for most of length, turning sharply upwards in the distal fifth. Margin delicate, circular to elliptical, with a pair of lateral lobes, aperture of immature hydrotheca closed by a delicate membranous flap.

Colonies dioecious, gonotheca large, situated beside a hydrotheca, male and female similar in shape and size, irregularly ovate, strongly flattened and adnate to the substrate by a wide peripheral flange, aperture distal, circular to subcircular, with thickened rim, the surface with small chitinous spines.

Colour. In life, colonies yellow or white, gonophores cream-coloured.

Remarks. In lateral view, the hydrothecae of sterile colonies of *L. flexuosa* may be mistaken for *Filellum*, particularly if the margins of some hydrothecae are circular and lack lateral lobes (Fig. 1D). Marginal lobes are, however, present

in most hydrothecae; these are best seen when viewed from above.

The most important difference between *L. spinulosa* and *L. flexuosa* is the presence of the basal hydrothecal spine in the former and its absence from the latter.

The hydrorhiza of *L. flexuosa* is narrower than that of *L. spinulosa* and is usually undulating, following the irregularities of the algal thallus, whereas that of *L. spinulosa* is flat, more orderly, and neatly aligned with the reticulating cells of the seagrass leaf.

The hydrothecae of *L. flexuosa* usually grow at an acute angle to, or sometimes parallel with the hydrorhiza, whereas those of *L. spinulosa* almost invariably project at right angles to the hydrorhiza. These structural differences may be environmentally induced and are thus not of specific importance. The hydrothecae of the two species are similar in shape but those of *L. spinulosa* are usually slightly larger. In both species usually only the distal fifth is bent upwards from the substrate, but in some hydrothecae one-third may be free.

Both species grow on a basal sheet of perisarc which separates the entire colony from the substrate. The underside of the hydrorhiza of *L. spinulosa* has numerous small, hook-like extensions that penetrate between the cells of the seagrass leaf, thus providing additional anchorage to the substrate. Although also present in *L. flexuosa*, hydrorhizal hooks are usually less well developed than in *L. spinulosa*, and they may be absent altogether.

There are no features that readily distinguish the gonothecae of the two species, except that the mature gonotheca of *L. spinulosa* is usually somewhat larger and has fewer spines than that of *L. flexuosa*.

When considered together these points of difference are sufficiently constant to warrant separation of the two species at present.

Because of the minute size and transparency of the hydrothecae, both species are easily overlooked.

Nicoliana gen. nov.

Type species. *Lineolaria gravierae* Millard, 1975.

Diagnosis. Colonies stolonial, hydrotheca sessile, deep, cylindrical to saccate, margin upturned, circular, with a peaked operculum of converging segments. Nematophores present. Gonotheca sessile, gonophore a fixed sporosac.

Remarks. *Nicoliana* differs from *Lineolaria* in

its segmented, conical operculum and the nematophores flanking the hydrotheca and gonotheca.

Nicoliana gravierae (Millard, 1975)

Fig. 1E-G

Lineolaria gravierae Millard 1975: 134, fig. 43H.

Lineolaria sp.—Gravier 1970: 144, figs 11, 13A.—Gravier-Bonnet 1972: 8.—Millard & Bouillon 1974: 22, fig. 2D.

Remarks. *Nicoliana gravierae* was described in detail by Millard (1975); it is figured here but not redescribed. It is one of the dominant epiphytic hydroids on the leaves of the seagrasses *Cymodocea serrulata* and *C. ciliata* from Madagascar (Gravier 1970, Gravier-Bonnet 1972), and is also reported from *Cymodocea* in Mozambique (Millard & Bouillon 1974, Millard 1975).

DISTRIBUTION AND EVOLUTION OF THE LINEOLARIIDAE

The success of *L. spinulosa* as a seagrass epiphyte suggests a long history of association with the Australian seagrass flora which may date back to the ancestral *Cymodocea serrulata* meadows of the Indo-Pacific Miocene. The present disjunct distribution and evolutionary isolation of the Lineolariidae between south-eastern Australia and southern Africa could be explained by later scattering of the shelf seagrass flora through continental break-up (Laurent & Laurent 1926, Larkum & den Hartog 1989). The apparent absence of the Lineolariidae from the eastern shores of the Indian Ocean in south-western Australia is nevertheless puzzling and requires further explanation.

L. flexuosa in south-eastern Australian waters may represent a case of incipient speciation from the ancestral *L. spinulosa* stock, leading to suppression and loss of several morphological characters. The habitat on algae is analogous to that of *L. spinulosa* on seagrasses since it also occurs in shallow coastal environments, often adjacent to seagrass meadows.

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